

Frontal dynamics boost primary production in the summer stratified Mediterranean Sea

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Abstract Bio-physical glider measurements from a unique process-oriented experiment in the Eastern Alboran Sea (AlborEx) allowed us to observe the distribution of the deep chlorophyll maximum (DCM) across an intense density front, with a resolution (~ 400 m) suitable for investigating sub-mesoscale dynamics. This front, at the interface between Atlantic and Mediterranean waters, had a sharp density gradient ($\Delta\rho \sim 1$ kg/m³ in ~ 10 km) and showed imprints of (sub-)mesoscale phenomena on tracer distributions. Specifically, the chlorophyll-a concentration within the DCM showed a disrupted pattern along isopycnal surfaces, with patches bearing a relationship to the stratification (buoyancy frequency) at depths between 30 and 60 m.

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In order to estimate the primary production (PP) rate within the chlorophyll patches observed at the subsurface, we applied the Morel and André (1991) bio-optical model using the Photosynthetic Active Radiation (PAR) from Argo profiles collected simultaneously with glider data. The highest production was located concurrently with domed isopycnals on the fresh side of the front, suggestive that (sub-)mesoscale upwelling is carrying phytoplankton patches from less to more illuminated levels, with a contemporaneous delivering of nutrients. Integrated estimations of PP ($1.3 \text{ g C m}^{-2} \text{ d}^{-1}$) along the glider path are two to four times larger than the estimations obtained from satellite based algorithms, i.e. derived from the 8-days composite fields extracted over the glider trip path. Despite the differences in spatial and temporal sampling between instruments, the differences in PP estimations are mainly due to the inability of the satellite to measure DCM patches responsible for the high production. The deepest (depth > 60 m) chlorophyll patches are almost unproductive and probably transported passively (subducted) from upper productive layers.

Finally, the relationship between primary production and oxygen is also investigated. The logarithm of the primary production in the DCM interior ($\text{Chl} > 0.5 \text{ mg/m}^3$) shows a linear negative relationship with the Apparent Oxygen Utilization, confirming that high chlorophyll patches are productive. The slope of this relationship is different for Atlantic, mixed interface waters and Mediterranean waters, suggesting the presence of differences in planktonic communities (whether physiological, population or community level should be object of further investigation) on the different sides of the front. In addition, the ratio of optical backscatter to Chl is high within the intermediate (mixed) waters, which is suggestive of large phytoplankton cells, and lower within the core of the Atlantic and Mediterranean waters. These observations highlight the relevance of fronts in triggering primary production at DCM level and shaping the characteristic patchiness of the pelagic domain. This gains further relevance considering the inadequacy of optical satellite sensors to observe DCM concentrations at such fine scales.

Keywords Primary production · Glider · Mediterranean Sea · Fronts · submesoscale · AOU

1 Introduction

Primary production in seas and oceans is crucial for both ecosystem functioning, since it regulates the available energy for higher-trophic-levels, and global warming, as it affects carbon export and sequestration. An interesting scientific debate is on the table about the mechanisms behind bloom initiation in temperate regions, classically explained by the seminal Critical Depth theory by Sverdrup (1953). Some recent studies proposed alternative (Behrenfeld, 2010, Dilution Recoupling hypothesis) or complementary (Huisman et al, 1999; Chiswell, 2011; Taylor and Ferrari, 2011a, Critical Turbulence) explanations of the bloom onset and the modulation of the primary production during the spring bloom. Other recent studies focused on the role of mesoscale and submesoscale dynamics in the crucial phase of bloom or early-bloom triggering (Mahadevan et al, 2012; Taylor and Ferrari, 2011b), emphasizing the relevance of dynamical processes at various scales in creating the conditions for producers to exceed consumption/export.

15 A short and focused synthesis of this debate was recently provided by Franks
16 (2014) while Chiswell et al (2015) attempted to shed light on these apparently
17 mutually exclusive theories through a simple theoretical model reproducing the
18 annual cycle of phytoplankton and checking how the model behavior could be ex-
19 plained by such different theoretical frames.

20 While the above-mentioned debate remains open, even less is known about the
21 mechanisms driving and controlling primary production, and its related biomass,
22 during the post-bloom period, i.e. during summer stratification and before the
23 onset of winter mixing and disruption of such stratification.

24 In temperate areas, once the seasonal thermal stratification has set in, the newly
25 formed upper mixed layer (UML) becomes naturally nutrient depleted. The phyto-
26 plankton community continues to live and reproduce in sub-surface layers, tightly
27 associated with the nitracline. It is commonly assumed that this layer is within
28 the pycnocline, below the UML, forming the so called deep chlorophyll maximum
29 (DCM, hereafter) otherwise called sub-surface maximum. This is an ubiquitous
30 feature of temperate regions of the world oceans. Processes and mechanisms un-
31 derlying the vertical position of the DCM in the different parts of the world oceans
32 and seas have been explored (Hodges and Rudnick, 2004), but still unclear. Re-
33 cently Navarro and Ruiz (2013) observed a tight relationship between the potential
34 density of the waters in which the spring bloom appears and the DCM pycnal lo-
35 cation, suggesting that the DCM localization would be better described in the
36 vertical using isopycnal coordinates than fixed depth levels. Primary production
37 associated with the DCM has been less explored than its winter-spring counter-
38 part, when surface blooms have been broadly assessed both in biomass and pro-
39 duction through satellite based studies (e.g. Antoine et al, 1996; Behrenfeld and
40 Falkowski, 1997). Satellite optical sensors are able to provide data up to $\sim 1/5$ of
41 the euphotic depth (Siswanto et al, 2005). This implies that algorithms for esti-
42 mation of integrated (throughout the euphotic depth) primary production usually
43 rely on a uniform vertical distribution of the Chl (here used as proxy for phyto-
44 plankton biomass) (e.g. Platt, 1986) for the "mixed" case (winter conditions) or
45 on a Gaussian vertical distribution to mimic the DCM conditions (e.g. Platt et al,
46 1991). Gaussian modeling actually can mimic DCM presence, but is not able to
47 describe the peaks often responsible for DCM and also visible in the present data.
48 We consider that the DCM outcropping events are not frequent enough so as to
49 imprint the average satellite perception sufficiently to account for the persistent
50 DCM maximum PP. The present case is a clear example where the DCM was
51 brought close to the surface, yet, the PP underestimation by the satellite remains.
52 On the contrary, in these case such underestimation can be even larger, consider-
53 ing that in normal conditions gaussian modeling can mimic DCM presence but in
54 presence of strong vertical dynamics as along frontal regions.

55 In the Mediterranean Sea the DCM was firstly investigated during the early
56 nineties of the past century (e.g. Varela et al, 1992; Delgado et al, 1992; Raim-
57 bault et al, 1993). Estrada (1996) found chlorophyll-a concentrations exceeding
58 2 mg/m^3 in the Balearic area, recording a tight relationship of the DCM position
59 with the nitracline depth. Very close to the location of the present study (Alboran
60 Sea), Moran et al (2001) found DCM of about 1.4 mg/m^3 through a mesoscale
61 resolving sampling cruise based on CTD and bottle measurements in October
62 1996. Authors estimated in the same study production maxima not exceeding 2
63 $\text{g C m}^{-2}\text{d}^{-1}$. Similar values of productivity were found by Videau et al (1994) for

64 the close Almeria-Oran front in the same period of the year while Rodríguez et al
65 (1998) showed that mesoscale features shape the size-structure of the phytoplank-
66 ton community in the Alboran Sea. Moreover, idealized modelling studies report
67 up to ten fold local increases of productivity by submesoscale dynamics in frontal
68 regions (Lévy, 2008; Lévy et al, 2012) due to large vertical velocities (Mahadevan
69 and Tandon, 2006). This dynamics can be specially relevant during stratified pe-
70 riods, when phytoplanktonic biomass concentrates in low-light layers.
71 In this framework, the new generation of underwater autonomous vehicles assume
72 an important role as they are able to resolve the submesoscale phenomena, acting
73 at 1-10 km scales. In the present study, high-resolution bio-physical observations
74 (temperature, salinity, fluorescence, turbidity, and dissolved oxygen) were collected
75 by a Slocum glider that traversed an intense front in the eastern Alboran Sea.
76 Glider measurements captured the sub-mesoscale distribution of the DCM across
77 the intense density front, which highlights the role of frontal dynamics. Primary
78 production estimates, obtained through a bio-optical model based on the glider
79 data and synchronous bio-Argo measurements (PAR, Chl, Oxygen, Temperature,
80 Salinity, Turbidity), allowed us to associate local frontal processes with production
81 and export estimates. Analysis of dissolved oxygen profiles also provided impor-
82 tant information on the biological and physical processes occurring at the front,
83 supporting the interpretation of the bio-optical primary production estimates.

84 **2 Materials and Methods**

85 **2.1 Gliders**

86 Two gliders, a deep and shallow Slocum glider (hereafter DG and SG respectively),
87 were deployed during the interdisciplinary, multi-platform process oriented study,
88 AlborEx (Ruiz et al, 2015; Pascual et al, 2017), carried out during the period 25-31
89 May, 2014 (see Fig.1). Gliders SG and DG profiled to a depth of 200 m (as part of
90 the Jerico-TNA proposal denominated FRIPP) and 500 m, respectively, measuring
91 temperature, salinity, oxygen, turbidity and fluorescence. The sampling strategy
92 was based on two parallel north-to-south transects, 10 km apart. Intense currents,
93 related to the frontal area, advected gliders eastward and the sampling strategy
94 (initially planned as a repeated round trip along the same route) was modified
95 in real time. Gliders performed several transects crossing the frontal zone, but
96 also moving eastward following the main stream direction, bordering an eddy. SG
97 sampled the ocean at an approximate horizontal resolution (at surface) of 0.4 km
98 (about 1 km for DG), thus achieving approximately 38 (14 for DG) dives per day.
99 Glider data processing includes thermal lag correction for salinity following the
100 methodology described in Garau et al (2011).

101 **2.2 Profiling floats**

102 During AlborEx, three profiling floats (Arvor-C, Arvor A3 and Prov-Bio) were
103 deployed in a straight line along the frontal zone, a few kilometers apart from
104 each other. The Arvor-C was programmed with 3h cycles down to 400 m. The
105 Arvor-A3 was initially configured to have daily cycles. At the end of the cruise, it

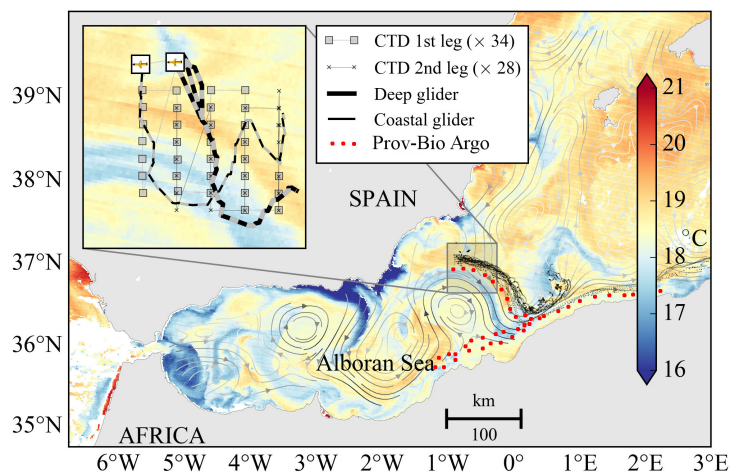


Fig. 1 Sampling strategy of AlborEx experiment: Glider, CTD and Prov-Bio float tracks are shown. Modified from Pascual et al (2017).

106 was left at sea and its cycle was changed to 5 days (MedArgo standard, Poulain
 107 et al, 2007) using the downlink of the Argos 3 telemetry. Both the Arvor-C and
 108 Arvor-A3 measured temperature and conductivity (salinity) in the water column.
 109 The Prov-bio float had initial daily cycles synchronized to profile near local noon
 110 time. It was left at sea after the campaign and its cycle was changed to 5 days
 111 using the Iridium downlink. In addition to temperature and salinity, the Prov-bio
 112 measured dissolved oxygen, Chlorophyll-a (converted from fluorescence), CDOM,
 113 backscattering at 700 nm, downwelling irradiance at 380, 410, 490 nm and PAR.
 114 The Prov-bio float measurements have been essential in order to calibrate an
 115 empirical model to estimate PAR from depth and Chlorophyll-a (Chl, hereafter)
 116 concentration (together with surface PAR obtained from atmospheric models, see
 117 below) collected by the gliders.

118 2.3 Bottle samples and Chl measurements

119 Samples for Chl and nutrients (NO_2^- , NO_3^- , PO_4^{3-}) analysis were collected during
 120 the cruise at eight depths (5, 20, 40, 60, 90, 100, 120, 150 m) in 66 stations, using
 121 10 L Niskin bottles mounted on a Sea-Bird SBE32 rosette sampler. At each station
 122 and depth one liter of water was filtered through a Whatman GF/F glass fiber
 123 filter for total Chl estimation. Chlorophyll concentrations were determined fluo-
 124 rimetrically (Holm-Hansen et al, 1965) using a Trilogy Turner Design fluorimeter
 125 after pigment extraction with 90% acetone for 24 hours in the dark at 4°C.

126 Although bottle data are not the focus of the present study, chlorophyll bottle
 127 measurements provided reference values to compare with glider-based estimates of
 128 Chl, as both Glider and float fluorimeters were originally calibrated by the manu-
 129 facturer and no cross-calibration was performed before the cruise. Chl maxima de-
 130 tected through bottle measurements are comparable (slightly exceeding 5 mg/m^3)
 131 to Chl maxima estimated through the fluorimetric method by the DG samplings

132 (see Fig.2). SG records of chlorophyll maxima are lower than DG records, with
 133 values of about 3.5 mg/m^3 , comparable to values found by Moran et al (2001).
 134 The discrepancy of the values between the two Gliders might be related to the
 135 spatial and temporal variability of the Chlorophyll field. The Chl measurements
 136 performed with the three different platforms (2 gliders, Prov-Bio Argo float, bottle
 137 direct measurements) are comparable in terms of density distribution and magni-
 138 tude (all platforms showing maxima around 5 mg m^{-3}).

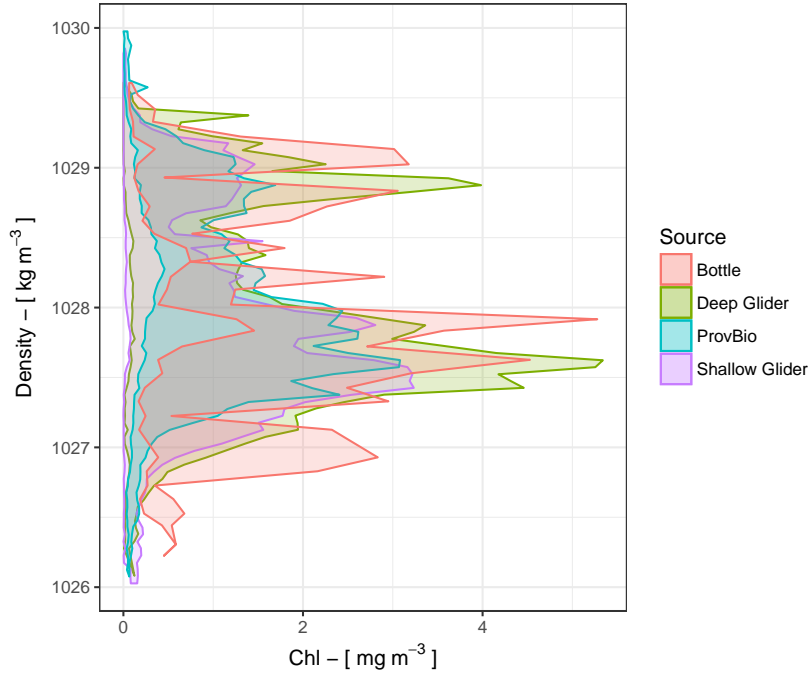


Fig. 2 Density distribution of Chl retrieved by the different sampling platforms. Shaded area depicts the range between Chl extrema evaluated for the different data sources within 0.05 kg m^{-3} density bins (0.1 kg m^{-3} for bottle samples). It deserves to be noticed that samples are collected in the same period and area but are not perfectly co-located both in time and space. Sampled scales also varies between sources.

139 2.4 PAR vertical distribution

140 The depth distribution of photosynthetically active radiation (PAR, $\mu\text{E m}^{-2} \text{ s}^{-1}$)
 141 is expressed as a bimodal attenuation function (Zielinski et al, 2002):

$$PAR(z) = PAR(0) \cdot \left(p_s \cdot e^{-\int_0^z k_s(z') dz'} + (1 - p_s) \cdot e^{-\int_0^z k_l(z') dz'} \right), \quad (1)$$

$$k_s(z) = k_{s,sw} + k_{s,chl} \cdot Chl(z), \quad (2)$$

$$k_l(z) = k_{l,sw} + k_{l,chl} \cdot Chl(z), \quad (3)$$

142 with short-wave fraction $p_s = 0.806$; sea-water attenuation coefficient for short
 143 and long-waves component $k_{s,sw} = 0.05295 \text{ m}^{-1}$ and $k_{l,sw} = 3.189 10^{-6} \text{ m}^{-1}$, re-
 144 spectively; short and long wave chlorophyll specific attenuation $k_{s,Chl} = 0.03328$
 145 $\text{m}^2 (\text{mg Chl})^{-1}$ and $k_{l,Chl} = 7.23 \text{ m}^2 (\text{mg Chl})^{-1}$, respectively. These five param-
 146 eters were calibrated to reproduce the PAR profiles measured by the Prov-bio
 147 float using the R FME package (Soetaert and Petzoldt, 2010). More details are
 148 provided in the Appendix. $Chl(z)$ is provided in situ from glider fluorescence data
 149 (and float fluorescence sensor for the model calibration phase). The surface PAR
 150 value was obtained from the ECMWF ERA-interim 6-hourly dataset. Such a sur-
 151 face PAR dataset was then resampled in time and interpolated in space to match
 152 the temporal and spatial framework of the glider.

153 2.5 Primary Production

154 Primary production has been estimated through a bio-optical method (Morel and
 155 Andr e, 1991; Antoine et al, 1996). In particular, (4) was applied for instantaneous
 156 synoptic estimations of primary production rates:

$$PP(z, t) = 12 Chl(z, t) a^*(z, t) PAR(z, t) \phi_\mu(z, t) \quad (4)$$

157 where Chl is the measured concentration of Chlorophyll-a in g Chl m^{-3} ; a^* is
 158 the specific absorption of phytoplankton, expressed as $\text{m}^2 (\text{g Chl})^{-1}$; PAR is the
 159 irradiance expressed as $(\text{mol quanta}) \text{m}^{-2} \text{s}^{-1}$ and ϕ_μ represents the transforma-
 160 tion efficiency expressed as $\text{mol C} (\text{mol quanta})^{-1}$. The PP instantaneous rates
 161 are converted from mol C to g C by using the carbon molar weight, which is 12
 162 $\text{g C} (\text{mol C})^{-1}$.

163 In our specific application PP was computed as function of depth (z) and time
 164 (t). Space(y) was used for convenience as frame of reference in plotted glider sec-
 165 tions instead of time (t). We neglected the wavelengths (λ) discretization (Morel
 166 and Andr e, 1991; Antoine et al, 1996; Hemsley et al, 2015). As reported by Hems-
 167 ley et al (2015), this can imply an underestimation of depth-integrated PP values
 168 up to 50% in respect to the use of discretized wavelengths. Nevertheless, Zielinski
 169 et al (2002) showed that the bimodal approach to reconstruct the underwater light
 170 field (used in the present study to reconstruct the PAR profile) is comparable to
 171 the multiband approach by Antoine et al (1996) in terms of ability to model the
 172 DCM concentration. Furthermore, and most important, the bimodal model for
 173 PAR showed the best fitting with observed vertical PAR (see appendix).
 174 This instantaneous PP ($\text{g C m}^{-3} \text{s}^{-1}$) can be integrated in time and depth to
 175 obtain PP estimations dimensionally comparable with satellite based estimates
 176 ($\text{g C m}^{-2} \text{d}^{-1}$).

177 For a^* we used the standard value of $0.01 \text{ m}^2 (\text{g Chl})^{-1}$ as proposed by Morel
 178 and Andr e (1991), which was also used in a glider based study of the PP in the
 179 North Atlantic (Hemsley et al, 2015). Concerning ϕ_μ , we used the formulation
 180 reported by Antoine et al (1996)

$$\phi_\mu = \phi_{\mu,max} f(x), \quad (5)$$

181 where the transformation yield is equal to the maximum yield $\phi_{\mu,max}$ (here set
 182 equal to $0.06 \text{ mol C} / \text{mol quanta}$ scaled by the function $f(x)$ (defined within 0 and

183 1), where $x = PUR/KPUR$ and $f(x) = \frac{1-e^{-x}}{x}e^{-\beta x}$. Here, PUR is the Photosyn-
 184 thetically Usable Radiance while $KPUR$ is a scaling irradiance. β is a dimension-
 185 less parameter for photoinhibition set to 0.01 (Hemsley et al, 2015). $KPUR$ is
 186 set as function of in situ temperature, also collected by the glider, following the
 187 expression (e.g. Hemsley et al, 2015):

$$KPUR(T) = KPUR(20^\circ) 1.065^{(T-20^\circ)} \quad (6)$$

188 We performed two separate computations of depth resolved PP: the first PP
 189 estimation was computed in the instrument sampling space to provide a picture
 190 of the actual instantaneous production in the glider space and time frame (PPg
 191 hereafter). In order to get such ephemeral rate comparable with a more conserva-
 192 tive quantity as the Apparent Oxygen Utilization (AOU), we also computed a
 193 noon Primary Production (PPn) i.e. assuming that the glider sampled instanta-
 194 neously at noon of each day. So in PPn computation the time (t) dependency is
 195 substituted by a space (y) dependency. PPn calculation allows to relate a non con-
 196 servative quantity, as Primary Production is, with other variables such as the AOU
 197 shaped by the biological history of the water mass under investigation. The rela-
 198 tion between these two quantities provides precious information on the underlying
 199 biological processes.

200 3 Results

201 3.1 The AlborEx context

202 The AlborEx experiment was carried out in the Eastern Alboran Sea, specifically
 203 at the edge of an anticyclonic mesoscale eddy (Pascual et al, 2017). This eddy was
 204 a persistent feature in the period immediately preceding AlborEx and during the
 205 sampling as well, as shown by time series of satellite single swath images in visible
 206 and infrared bands (Fig.3). The eddy shaped (advecting it and/or locally con-
 207 tributing to its production) the chlorophyll footprint in an anticyclonic curvature.
 208 This curvature, also visible in SST, is a characteristic imprint of a meandering jet
 209 of cold Atlantic waters (e.g. Tintoré et al (1988), Oguz et al (2014)) that enter the
 210 Alboran Sea through the Gibraltar Strait. These Atlantic waters (AW), circulated
 211 along the eddy periphery and entrained into Mediterranean waters (MW) in the
 212 north-eastern side of the mesoscale eddy, forming sharp gradients visible in SST.
 213 During the AlborEx experiment, gliders intercepted one of these filaments and
 214 unveiled remarkable chlorophyll subduction underneath them (Fig. 4), subduction
 215 reaching and exceeding 100 m depth in terms of chlorophyll signature.

216 3.2 Hydrography and deep chlorophyll maximum

217 In the following, the SG sampling is considered in virtue of its finer spatial resolu-
 218 tion reaching sub-mesoscale. AlborEx gliders sampled a sharp front in salinity at
 219 the confluence of Atlantic and Mediterranean waters (Fig. 5a). Such salinity gra-
 220 dient was the main responsible for a lateral density gradient of $\Delta\rho \sim 1 \text{ kg m}^{-3}$ in
 221 about 10 km (Fig. 5b). Subsurface chlorophyll patches within the DCM (Fig. 5c)

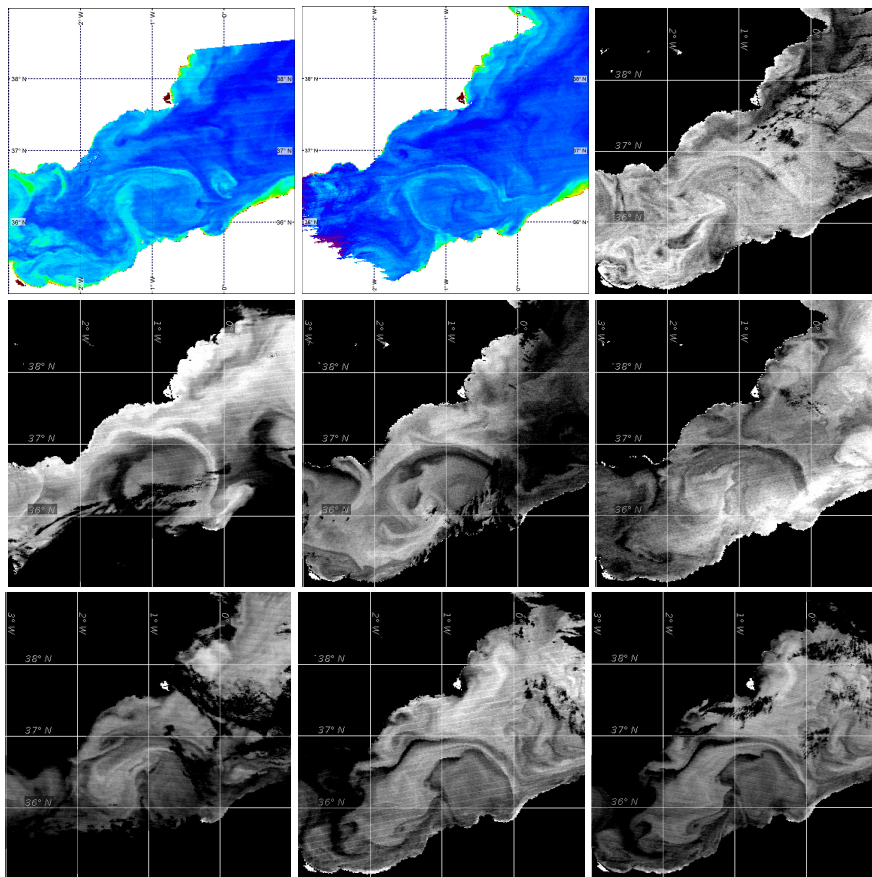


Fig. 3 Series of satellite data (MODIS Level-2 single swaths). First image (top left) is for May 3, 2014 and last image for May 30 (bottom right). Colored images are ocean color, black-white are SST. Left to right and top to bottom, days of May 2014: 3, 5, 12, 18, 21, 25, 27, 29, 30. The glider sampled the frontal/eddy system between May 25 and 30 (last four images).

222 reached extremely high concentration (up to 3 mg m^{-3} for SG and 5 mg m^{-3} for
 223 DG and bottles, see Sect. 2.3) in respect to usual values for the Mediterranean
 224 DCM, even in such strong frontal areas (cf. Moran et al, 2001, with maximum of
 225 1.4 mg m^{-3}).

226 The Chl distribution is strongly heterogeneous in both the horizontal and the
 227 vertical dimension, suggesting strong frontal dynamics. Such patchiness can be
 228 related to the static stratification of the water described by the buoyancy fre-
 229 quency. Chlorophyll contours of 0.5 mg m^{-3} (Fig. 5d) match quite well with the
 230 relative lows of buoyancy frequency within the 30–60 m layer. In the fresh side
 231 of the front, Chl patches were found across the mixed layer limit, defined with
 232 a density threshold of 0.03 kg m^{-3} (de Boyer Montégut et al, 2004) with respect
 233 to a sub-surface reference level at 20 m (shallowest depth of glider sampling). In
 234 contrast, in the high-salinity side of the front, deep patches ($> 60 \text{ m}$) are located
 235 well below the area of high stratification (high values of N^2). Large values of Chl
 236 are found concurrently with isopycnal doming on the fresh side of the front and

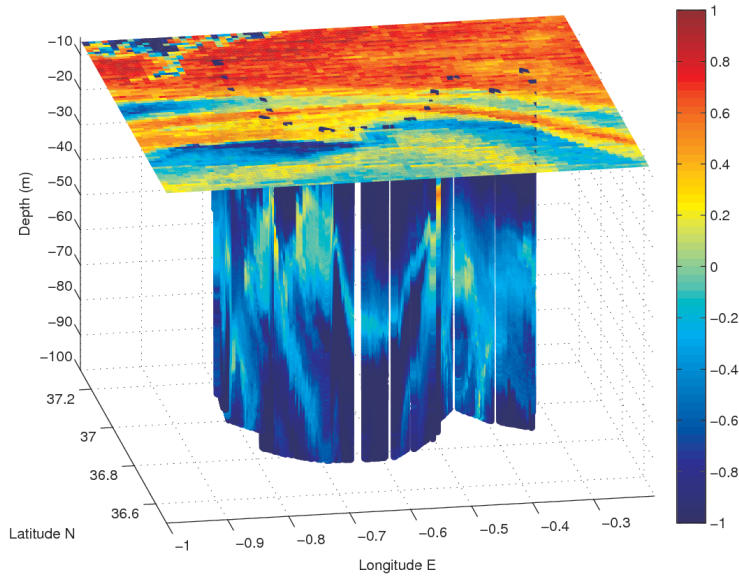


Fig. 4 SST field (the horizontal plane on the top) superimposed on the vertical Chl distribution detected by the SG glider. Units for SST are Celsius degrees $^{\circ}\text{C}$ from which have been subtracted -19°C (in order to keep a single palette and colorbar) and $\log(\text{Chl})$ in mg m^{-3} for Chl.

237 within the interface (i.e. not in the core of the fresh waters). Such doming suggest
 238 the presence of upwelling/downwelling motion along isopycnals, also confirmed by
 239 disruptions in stratification.

240 The vertical distribution of Chl seems primarily determined by the density of
 241 water masses and secondarily by the vertical motion of such water masses. Indeed,
 242 water mass density instead of depth allows to distinguish different "populations"
 243 (not in biological sense) of planktonic biomass distribution (Fig. 6). The relation
 244 with potential density discerns three different peaks respectively for MW, AW and
 245 interface waters. On the contrary, AW and MW peaks are partly superimposed in
 246 the Chl-depth relation.

247 3.3 Primary Production

248 Estimated primary production rates, both in the glider sampling frame (PPg,
 249 Fig.7a) and in the synoptic frame at noon (PPn, Fig.7b) are shown. It is evi-
 250 dent, as expected, that production patches are coincident with patches of high
 251 Chl concentration, in particular for the shallowest ones upwelled along isopycnals.
 252 Instantaneous values per unit of volume (converted in daily rates for convenience
 253 of representation) reach $0.5 \text{ g C m}^{-3} \text{ d}^{-1}$ for PPg and exceeds $0.8 \text{ g C m}^{-3} \text{ d}^{-1}$ for
 254 PPn.

255 Integrated quantities over the euphotic layer (defined as the depth at which
 256 PAR equals 1% of the surface value) for PPg estimates are reported in Tab. 1, to-
 257 gether with averaged values for the main satellite PP products (averaged along the
 258 glider track from the 8-days level-3 product covering the sampling period, please

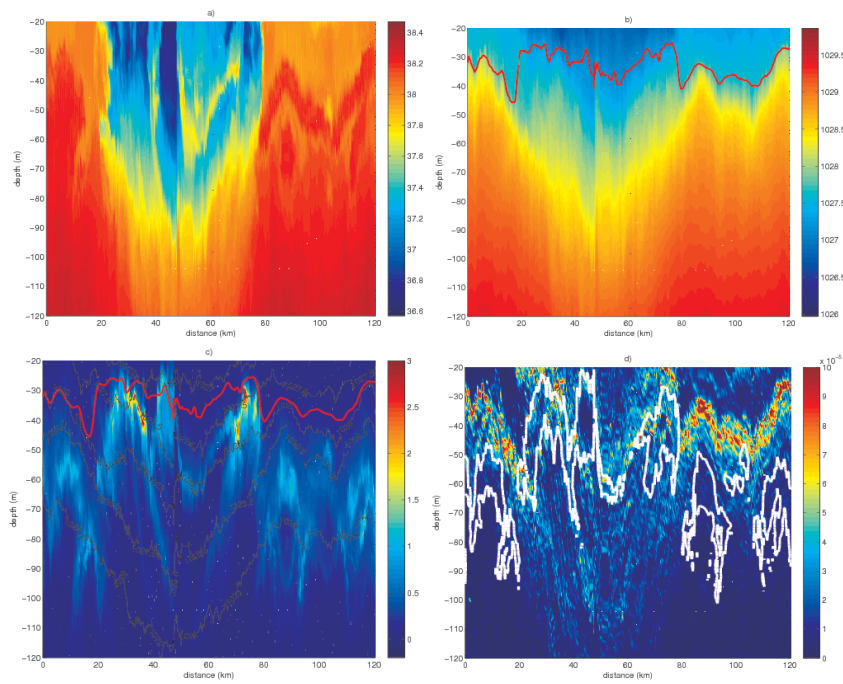


Fig. 5 a) Salinity; b) Density ρ , kg/m^3 , with MLD superimposed (red curve); c) Chlorophyll, mg m^{-3} , with superimposed isopycnals (grey curves); d) buoyancy frequency N^2 with the $\text{Chl}=0.5 \text{ mg m}^{-3}$ contour superimposed in white. Cross-front sections correspond to the coastal glider (see Fig. 1 for trajectory).

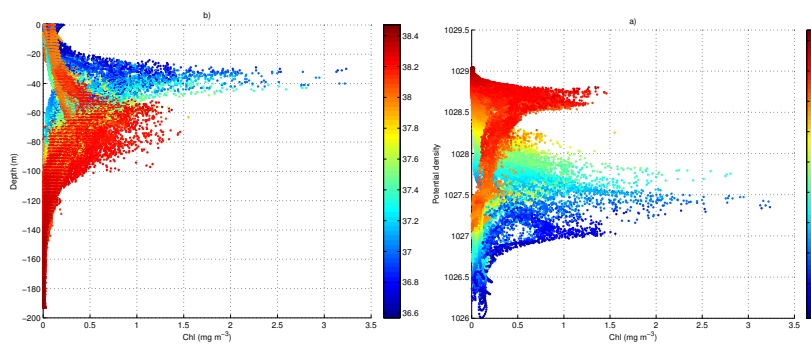


Fig. 6 Scatterplot of Chl (mg/m^3) vs a) depth (m); b) potential density (kg/m^3). For both panels, color is salinity. It is evident how chlorophyll peaks are better discerned in terms of potential density.

259 see <http://www.science.oregonstate.edu/ocean.productivity/> for satellite prod-
 260 ucts documentation). It is evident that satellite products tend to largely under-
 261 estimate Chl and PP values in frontal zones during the stratification period, i.e.
 262 when the light-limited production mainly takes place within the DCM and can be
 263 boosted at depth by uplifting mechanisms without strong surface manifestation.

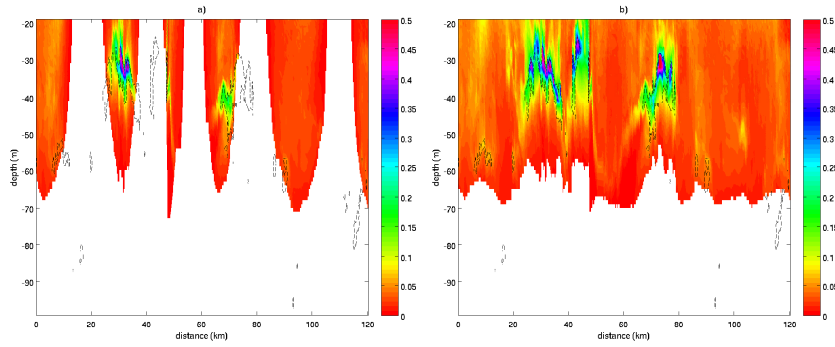


Fig. 7 Primary production estimates a) in the sampling space (PPg) and b) synoptic estimates at noon (PPn). In panel b) the x-axis is expressed in terms of "profiles" instead of "time" accordingly to the synoptic assumption done for PPn computations. Units are $\text{g C m}^{-3} \text{d}^{-1}$. Black dashed lines indicate 1 mg m^{-3} Chl contour.

Table 1 Vertically integrated primary production averaged along the glider track, considering present estimates (PPg) and three of the main products for PP freely distributed. Units are $\text{g C m}^{-2} \text{d}^{-1}$

PPg	sat VGPM	sat CBPM	sat Eppley
1.32	0.68	0.32	0.46

264 Such value, we remind strictly related to this particular front and sampling, on
 265 one hand exceeds in situ estimations of integrated production during spring period
 266 in high trophic areas of Mediterranean, as for instance the Gulf of Lyon (Lefevre
 267 et al, 1997, reporting integrated maxima of $0.5 \text{ g C m}^{-2} \text{d}^{-1}$). On the other hand,
 268 it is close to the largest estimations we found for integrated production during
 269 the stratification period for the NW Mediterranean (Estrada, 1996, with about 2
 270 $\text{g C m}^{-2} \text{d}^{-1}$) but retrieved in October, at the end of the stratification season.

271 3.4 Apparent Oxygen Utilization

272 Apparent Oxygen Utilization (AOU) helps in understanding the processes under-
 273 lying the observed Chl distribution and PP. AOU is computed as the difference
 274 between the theoretical (i.e. at saturation) and observed oxygen concentrations
 275 (expressed in $\mu\text{mol/l}$). It can be considered as a buffer diagnostic, which integrates
 276 in time the biogeochemical terms of oxygen dynamics in aquatic environments.
 277 Large negative values of AOU were found during the glider sampling (Fig. 8) from
 278 the surface down to the oxycline (here defined as the depth where the oxygen
 279 vertical gradient is the largest). In biologically active layers (such as the DCM
 280 and the mixed layer), such negative values indicate that oxygen production rates
 281 exceed consumption rates. The change of sign, negative to positive from surface
 282 to bottom, happens concurrently with centers of biological production located in
 283 the DCM, with steeper vertical AOU gradient in the AW (at the interface), and
 284 smoother gradient for the DCM located in the bulk of the MW (Fig. 8).
 285 A negative linear relationship is observed between AOU and $\log(\text{PPn})$ (Fig. 9, scat-

286 ter plot restricted to waters with large phytoplankton content, $\text{Chl} > 0.5 \text{ mg m}^{-3}$),
 287 supporting the validity of PP estimates. The slope of this relationship is steeper
 288 for mixed waters ($1027 < \rho < 1028.3 \text{ kg/m}^3$), where the largest production occurs
 289 (Fig. 8a), than for Mediterranean waters ($\rho > 1028.3 \text{ kg/m}^3$). The bulk of Atlantic
 290 waters ($\rho < 1027 \text{ kg/m}^3$) show an inverse relationship between AOU and $\log(\text{PPn})$.
 291 The milder slope in MW, where negative AOU values are associated with poorly
 292 productive layers, suggests the subduction of formerly productive waters to low-
 293 light layers on the Mediterranean side of the front, still preserving negative AOU
 294 values (i.e. oxygen supersaturation).

295 Figure 9b depicts the same relationship but colored as function of the backscat-
 296 tering/Chl ratio (Optical Community Index, Cetinić et al, 2015). Large values of
 297 this ratio indicate a larger probability for the prevalence of microphytoplankton
 298 and diatoms dominated communities, while small values the prevalence of pico
 299 and nano-phytoplankton. It is interesting to note that such ratio does not change
 300 between AW and MW, while it assumes large values (for the mixed waters with
 301 a density ρ of about 1027.5 kg/m^3 , cfr. with panel a) in coincidence with the
 302 largest PP values. Also, the lowest values of the Optical Community Index are
 303 found along the same cloud of points related to the mixed waters concurrently
 304 with low PP values. Accordingly to the findings of Ruiz et al. (submitted), the
 305 latter patches are being subducted due to submesoscale frontal dynamics along
 306 the interface between two water masses. Consequently, they are likely subject to
 307 acclimation (physiological and/or at community level) to the new light conditions.

308 These observations suggest that the physical environment, in these particular
 309 conditions, is able to shape the phytoplankton community at the sub-mesoscale
 310 ($1 - 10 \text{ km}$) and in coincidence with the frontal region, in agreement with recent
 311 observations reporting the sub-mesoscale spatial structuring of phytoplankton at
 312 population level (Mousing et al, 2016).

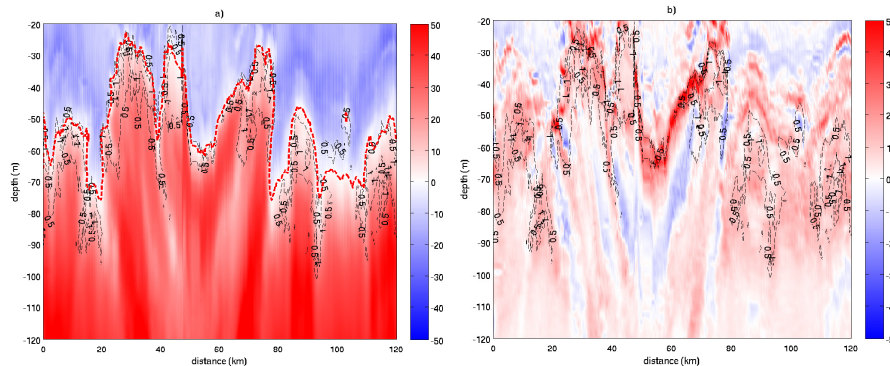


Fig. 8 a) Apparent Oxygen Utilization (AOU, $\mu\text{mol/l}$) distribution in the top 120 m. Thick red line is the zero AOU curve. b) AOU vertical gradient. Black dotted (labeled) lines on both panels corresponds to iso-contours of PPn.

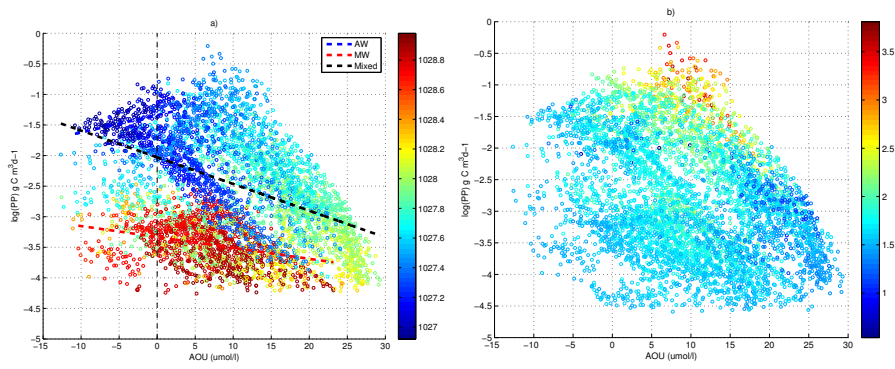


Fig. 9 Scatterplot of AOU vs log(PPn) colored as function of a) density (kg/m^3); b) Backscattering/Chl ratio (digital counts)

313 4 Discussion and Conclusions

314 The present study uses a set of high resolution bio-physical glider observations
315 (salinity, temperature, oxygen, fluorescence, turbidity) to investigate the impact
316 of frontal processes on the primary production associated to a Deep Chlorophyll
317 Maximum. The primary production is estimated using a methodological approach
318 similar to that presented by Hemsley et al (2015) in the North Atlantic. The two
319 main variations of this method here are the estimation of PAR radiation, which is
320 based on synchronous PAR observations performed through Argo floats, and the
321 use of a single irradiance value for PP algorithm (not discretized in λ bands).

322 DCM is known to be an ubiquitous feature that, in temperate regions, onsets af-
323 ter seasonal thermal stratification and consequent nutrient depletion of the top
324 mixed layer (Cullen, 1982). This simple theoretical frame for DCM formation and
325 functioning is complicated by presence and action of ubiquitous mesoscale and
326 sub-mesoscale structures. It was largely shown (cfr. McGillicuddy, 2016; Mahade-
327 van, 2016, for two reviews about impacts of mesoscale and submesoscale dynam-
328 ics, respectively) that (sub-)mesoscale features impact the biology through several
329 mechanisms. Nutrient uplift of nutrients; subduction of organic matter; dynamical
330 re-stratification (Taylor and Ferrari, 2011a; Mahadevan et al, 2012) are some of the
331 main processes impacting biogeochemistry and consequently biology at such scales.
332 Very little can be found in literature about the role of such dynamical features
333 in the modulation of the biological activity during stratification and DCM onset.
334 During stratification, while the ML is nutrient-limited the DCM is substantially
335 light-limited. At such low light conditions, photoacclimation processes may occur
336 (Lazzara et al, 1996; Mignot et al, 2014), determining an increase of the Chl con-
337 tent in cells and a possible decoupling of the biomass peak from the DCM (Mignot
338 et al, 2014). Given that the PAR reaching the DCM is usually between 1 and 10%
339 of the incident radiation at surface (Siswanto et al, 2005), it could be assumed a
340 weak contribution of DCM to total annual production. In this case, the error in
341 satellite-based production estimates, associated with the inability of space-borne
342 sensors to see the full euphotic water column and with the consequential need for
343 approximations (namely uniform or gaussian distributions of Chl along the water
344 column), could be actually negligible.

345 This picture can be drastically modified by the intervention of (sub-)mesoscale
346 dynamics, as observed in the present study. Biomass and production estimates
347 obtained in-situ during AlborEx are unusually high for such period of the year
348 in comparison to satellite-based estimations, notwithstanding the prudent ap-
349 proach we adopted in estimating primary production. The largest production is
350 observed concurrently with shallower phytoplankton patches, initially belonging
351 to the DCM level and therefore substantially light-limited, up-lifted to euphotic
352 depths by mechanisms related to mesoscale and to frontal (ageostrophic) dynam-
353 ics (Ruiz et al, 2017). The bio-optical estimations of large primary production
354 levels ($1.3 \text{ g C m}^2 \text{ d}^{-1}$) are supported by negative AOU values within the ML and
355 negative AOU/production relationship, having a different slope for the different
356 water masses. The steepest slope is found for mixed waters, which is indicative
357 of a tighter coupling between production and AOU, i.e. a more intense biological
358 activity.

359 It is quite instructive to look upon the vertical/pycnal distribution of Chl
360 through the lens of the hysteresis theory for DCM presented by Navarro and Ruiz

361 (2013). The Authors observed worldwide that the vertical position of the DCM
362 is better explained in terms of density, following the seasonal history of water
363 masses, than in terms of instantaneous physico-chemical, depth-related diagnostics
364 (eg. mixed layer depth, nutricline). In a few words, the density at which the DCM
365 forms during stratified conditions corresponds to the density of the previous winter
366 mixed layer bloom. The authors suggest that, during winter blooms, the planktonic
367 assemblage is tailored around the density conditions of the winter mixed layer,
368 and that this preference persists along the seasons and impress upon the vertical
369 position of the DCM during the stratified period.

370 Here, two water masses of distinct origins encounter forming a sharp front.
371 According to the hysteresis paradigm, they carry distinct populations, tailored to
372 distinct density levels, which is in agreement with the distribution pictured on Fig.
373 6b. In general, the uplifting of the AW DCM isopycnal in euphotic depths triggers
374 high primary production. But the highest PP occurs in mixed waters, i.e. on the
375 Atlantic, fresher, side of the front. Here, a change in the planktonic assemblage
376 (and/or a physiologic adjustment) is suggested by the Optical Community Index
377 (Fig. 9b). It could be speculated that favorable conditions (light and nutrients)
378 are met in a new density niche emerging at the front, which the dominant species
379 of the Med and Atlantic assemblages might not be used to exploit. This would
380 lead to a reorganization of the planktonic web structure (Mousing et al, 2016) in
381 which a new player is able to grow, unchallenged on these short time-frame.

382 Clearly, the preceding paragraph is highly speculative at this point. Our pri-
383 mary statement is that a sub-surface increase in the DCM production, substan-
384 tially unspotted from space, is caused by strong vertical motions at the front (Pas-
385 cual et al, 2017). This is directly supported by the presented results and does not
386 require any assumption regarding the reason behind the different DCM positions
387 in Atlantic and Mediterranean waters. Beyond that, our observations also suggest
388 that frontal dynamics might affect biogeochemical processes through strictly bio-
389 logical mechanisms and call for further investigations. Such efforts would have to
390 be supported by an AlborEx-like cruise but complemented with in-situ production
391 estimates and microscopic analyses to characterize planktonic populations.

392 The high production rates estimated along the frontal area, also previously
393 reported in the literature for frontal regions of the Alboran sea (Videau et al,
394 1994; Moran et al, 2001, with maxima of $\sim 2 \text{ g C m}^2 \text{ d}^{-1}$), may be relevant to better
395 understand the functioning of the Mediterranean ecosystem. It is still unclear, for
396 instance, how the Mediterranean can sustain a large yield of fish catches (and
397 thus a large secondary production) in front of a relatively low primary production
398 (Estrada, 1996). Could the chronic underestimation of the production related to
399 the DCM explain this issue? On the one hand, it could be argued that such large
400 values of production could be found only locally in the vicinity of intense fronts.
401 On the other hand, the entire southern part of the Western Mediterranean (the
402 Algerian Basin) is largely populated by mesoscale AW eddies and therefore frontal
403 structures at the periphery of these eddies, such as the one intercepted in our
404 study, may be ubiquitous in the area. The application of the present glider-based
405 methodology for PP estimation (properly calibrated) to a larger Mediterranean
406 dataset covering the eddy field of the Algerian Basin, during DCM conditions,
407 would substantially help to reply to the above question, still unresolved.

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 418 processing.

419

420 A Calibration of the optical model

421 The pragmatic objective of this section is to calibrate, on the basis of the Prov-Bio optical
 422 data (Sect. 2.2), an optical model suited to reconstruct the PAR conditions along the AlborEx
 423 coastal glider (SG) transect. For this specific objective, only the profiles obtained between the
 424 26st of May and the 7th of June were considered, when the Prov-Bio path was close to the
 425 AlborEx front.

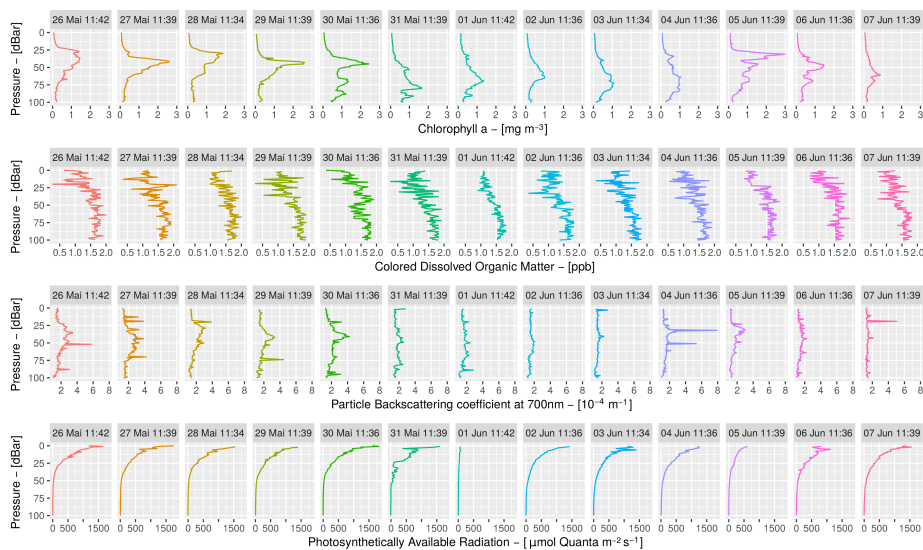


Fig. 10 Optical parameters recorded by the Prov-Bio floats near the AlborEx front.

426 Several candidate optical models were tested, considering a single bandwidth with Chl and
 427 CDOM attenuation (PAR_1), or two bandwidths (Zielinski et al, 2002) with attenuation from
 428 Chl only (PAR_2) or Chl and CDOM (PAR_3):

$$PAR_1 \begin{cases} PAR(z) &= PAR(0).e^{-\int_0^z k(z') dz'} \\ \text{with } k(z) &= k_0 + k_{Chl}.Chl(z) + k_{CDM}.CDM(z) \end{cases} \quad (7)$$

$$PAR_2 \begin{cases} PAR(z) &= PAR(0). \left[p_s.e^{-\int_0^z k_s(z') dz'} + (1-p_s).e^{-\int_0^z k_l(z') dz'} \right] \\ k_s(z) &= k_{s,0} + k_{s,Chl}.Chl(z) \\ k_l(z) &= k_{l,0} + k_{l,Chl}.Chl(z) \end{cases} \quad (8)$$

$$PAR_3 \begin{cases} PAR(z) &= PAR(0). \left[p_s.e^{-\int_0^z k_s(z') dz'} + (1-p_s).e^{-\int_0^z k_l(z') dz'} \right] \\ k_s(z) &= k_{s,0} + k_{s,Chl}.Chl(z) + k_{s,CDM}.CDM(z) \\ k_l(z) &= k_{l,0} + k_{l,Chl}.Chl(z) + k_{l,CDM}.CDM(z) \end{cases} \quad (9)$$

429 For the sake of simplicity, and since all profiles were taken at the same hour of the day in
 430 a 12-day interval, the incoming surface radiation was considered to be identical for all profiles
 431 and was tuned as a single parameter. Only two profiles were excluded for the calibration
 432 (corresponding respectively to the 1st and 5th of June) as they presented obviously affected
 433 incoming surface radiation, for instance due to cloud cover (Fig. 10).

434 The parameters of models PAR_1 , PAR_2 and PAR_3 were calibrated to reproduce at best
 435 the corresponding Prov-Bio PAR profiles, when applied on the concurrent Chl and CDOM
 436 data. The skill associated with each model is given as the root of the PAR mean squared
 437 residuals evaluated for all the selected profiles (i.e., 11 profiles consisting of ~ 215 measurement
 438 each) and are provided in Table 2).

PAR Model	Number of parameters	RMS
PAR_1	4	42.77
PAR_2	6	41.20
PAR_3	8	41.23

Table 2 Number of parameters and model skill evaluated for the optical models.

439 The consideration of two band widths in models PAR_2 and PAR_3 enhances the model
 440 skills. The consideration of CDOM in PAR_3 does not appears beneficial in what regards the
 441 model skill, and poses an additional question in terms of parameter identifiability.

442 We finally retained model PAR_2 , with parameters $PAR_0 = 1532 \mu E m^{-2} s^{-1}$; $p_s = 0.806$;
 443 $k_{s,sw} = 5.295 10^{-2} m^{-1}$; $k_{l,sw} = 3.189 10^{-6} m^{-1}$; $k_{s,Chl} = 3.328 10^{-2} m^2 mg Chl^{-1}$; $k_{l,Chl} =$
 444 $7.23 m^2 mg Chl^{-1}$;

445 The probability distribution around those values, as well as the dependencies between
 446 different parameter estimates, are depicted on Fig. 11 showing the distribution of parameter
 447 values retained in a Monte Carlo Markov Chain procedure (Soetaert and Petzoldt, 2010). The
 448 pairwise relationships between successful parameter sets indicate a strong correlation between
 449 the long-wave band attenuation coefficients for sea-water ($k_{l,sw}$) and Chl ($k_{l,Chl}$). In other
 450 terms, the good matching between simulated and observed PAR profiles is somewhat equivalent
 451 whether the long-wave band is attenuated by seawater or Chl. We retained the best parameter
 452 values indicated above, which gives a large weight to Chl for the long-wave attenuation, but we
 453 checked carefully that the PP estimates obtained from SG data were only marginally affected
 454 when using a parameter set in which long-band attenuation was driven by sea water.

455 The PAR_2 model provides a representation of the PAR profiles suitable for the next steps
 456 of this study (Fig. 12, with percentage residuals always below 50% and usually well below 25%
 457 in the upper 60 m, a depth below which PAR is always lower than 5% of the surface incoming
 458 radiation).

459 As the model calibration was restricted to AlborEx Prov-Bio input data we do not pretend
 460 that our conclusions concerning the optical model suitability apply, for instance, to the entire

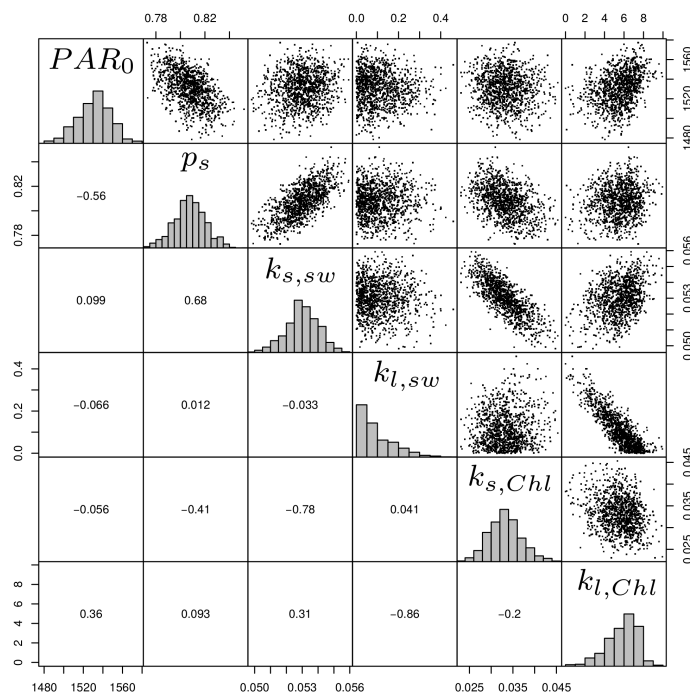


Fig. 11 Marginal parameter distributions (diagonal), pairwise relationship (upper panels) and correlation coefficients (lower panels) between parameters of the optical model PAR_2 , obtained by applying a Markov Chain Monte Carlo procedure as described in (Soetaert and Petzoldt, 2010). Note the strong relationship between the calibrated sea water and chlorophyll attenuation coefficient, in particular for the long-wave light band.

461 Mediterranean Sea, over which the concentrations of optically relevant water constituents vary
 462 on ranges much larger than those encountered here.

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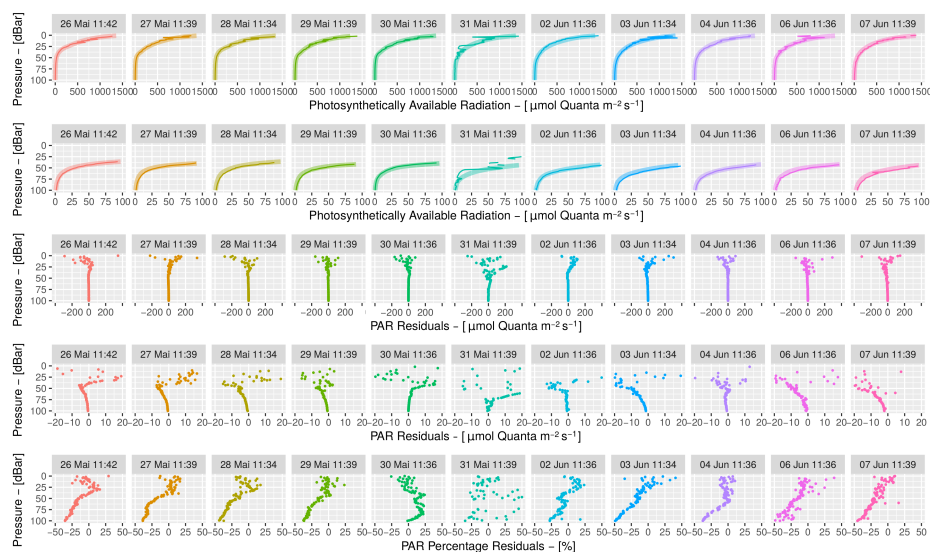


Fig. 12 PAR profiles reproduced by applying the PAR_2 function on Prov-Bio profiles. First and second rows presents (wide light line) modelled and (thin dark line) observed PAR profiles on different scales. Third and fourth rows present the corresponding residuals. The fifth row indicates the relative residuals, ie. $\frac{PAR_{model} - PAR_{obs}}{PAR_{obs}} \cdot 100$

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